ASPECTS OF THE SPECIES QUESTION

At the recent Chicago meeting of the Botanical Society of America, the afternoon of Wednesday, January 1, was devoted to a symposium on "Aspects of the Species Question." The principal participants, who, upon invitation of the council, prepared and read papers at the symposium, were: C. E. Bessey and N. L. Britton, who discussed the taxonomic aspect; J. C. Arthur and D. T. MacDougal, who spoke on the physiologic aspect; F. E. Clements and 'H. C. Cowles, who dealt with the ecologic aspect of the question. The reading of the papers was followed by an open discussion of the question by a number of the members present. The papers read and the corrected stenographic report of the discussion are printed below.

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D. S. Johnson,
Secretary.

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THE TAXONOMIC ASPECT OF THE SPECIES QUESTION

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As long as species were supposed to be actual things, "created as separate kinds at the beginning," that botanists "discovered," as explorers discover islands in the ocean, there was no serious "species question." A botanist might make a mistake, and announce the discovery of a new species, when he had merely found a variety of an old species; as an explorer might mistakenly announce the discovery of a new island, when as a matter of fact he had only seen an unfamiliar coast of a long-known island.

Nature produces individuals, and nothing more. She produces them in such countless numbers that we are compelled to sort them into kinds in order that we may be able to carry them in our minds. This sorting is classification—taxonomy. But right here we are in danger of misunderstanding the matter. We do not actually sort out our individuals. We imagine them sorted out. It is only to a very slight extent that the systematic botanist ever actually sorts out individuals. When he has a considerable number of individual dried plants in his herbarium, he may sort them out, but these are but an infinitesimal portion of all the individuals in the world that we imagine to be sorted, but that are actually unsorted.

So species have no actual existence in nature. They are mental concepts, and nothing more. They are conceived in order to save ourselves the labor of thinking in terms of individuals, and they must be so framed that they do save us labor. If they do not, they fail of

their purpose. Here we perceive one of the principles
which must control in the limitation of species. If we
multiply our species unduly we approach too near to the
individuals, and we are as much burdened as though we
had not invented species. On the other hand, if we make
too few species those we do make include so many varia-
tions from the type that confusion results again.   We
must steer a course between these two extremes.

I am well aware that every man who has split up
species upon any pretext will at once lay his hand upon
his heart and assure himself that he has done this very
thing of avoiding these extremes. I have yet to find a
man who has not felt that all of his species were con-
servatively made, and that had he been radically inclined
he could have made many more. And yet the fact re-
mains that much of the species-making of recent years
has rendered it vastly more difficult than formerly for
us to obtain a grasp of the flora of a region. Instead of
helping us, this perverted notion of the purpose and the
proper limitation of species has actually proved to be a
hindrance. How much, for example, does the average
botanist know nowadays about the species of Cratægus?
It will not avail to say that "he knows as much as he ever
did," for once he did study them somewhat, but now he
is compelled to pass them by as quite too difficult for him
to undertake to distinguish with the time he has at his
command. The inordinate multiplication of species has
hindered instead of advanced our knowledge, and this
fact is sufficient to condemn it utterly.

We are in danger of destroying the usefulness of tax-
onomy in our zeal for describing every differing form
as a separate species. We have lost sight of the prim-
itive reason for the formation of species, namely, that
we should have fewer things to hold in mind. Primitively
the aim was to have as few species as possible. Now
too often we look upon the addition of new species as a
contribution to knowledge, when, on the contrary, it may
be a hindrance.

The Linnean conception of species may have been too broad, but it had the merit of being understood. It has yet to be shown that that conception of species has been outgrown. The human mind is pretty nearly the same to-day that it was a century and a half ago. The botanists of to-day may be able to recognize species where Linné, and DeCandolle, and Gray could not, but the difference is by no means great enough to warrant such great changes as have taken place in the conception of species by some recent systematists. The human mouth is probably a little smaller than it was thousands of years ago, and probably the tendency is to a reduction of its dimensions, but it certainly has not changed so much as to warrant a marked reduction in the size of tablespoons; much less does it give sanction to any proposal to reduce them to the size of miniature saltspoons! The old spoons that still fit the average human mouth very well are not likely to be displaced for much smaller ones. I think it is highly probable that in like manner we shall insist upon the old measure of species, for the good reason that it is still well fitted to our mental needs and mental capacity. The experience of botanists as a body sanctions the general idea and limitations of species as understood by Linné, by DeCandolle, by Gray, rather than that of the species-makers of recent years. This sanction is not in deference to authority, but for the reason that their species commend themselves to us. We prefer the Linnean idea of species not because it is Linnean, but because it is more useful than those proposed more recently. Probably one reason for the vogue of the Linnean conception of species for the past century and a half is that it is so well adapted to the mental requirements of botanists the world over. Linné was fortunate in adopting a measure of species which was neither so small as to be difficult to apprehend, nor so large as to be cumbersome. It may have been by happy chance that he hit upon this acceptable measure of species; it is much more likely that it was but another

example of that genius which gave him such great pre-eminence among the botanists of his day, and enabled him to make so lasting an impression upon systematic botany.

We have given a good deal of attention to the laws of botanical nomenclature, a matter of considerable, but by no means paramount, importance, while we have pretty largely neglected the far more important laws of botanical taxonomy.   We have legislated at length in regard to names of species, genera, families, orders, and so on to the end of the list, while we have scarcely touched upon the far more important question of what these groups should be.   We have been more concerned with the chaff than with the wheat itself.

We are forced to the conclusion that we have rather foolishly spent our time in discussing the less important matters of nomenclature, while we have permitted anarchy to thrive in the far more important work of the making of species.   We have had botanical congresses which formulated laws in regard to the *naming* of species, but as to the *making* of species each botanist is allowed to follow his own notions without any guide whatever, and what is worse still, without any restrictions.   The result is what we should expect.   It is confusion; it is scientific anarchy.   If an indefinite number of men were to contribute stones for a building, there being no agreement among them as to shape or dimensions, what would be the result?   No worse, I am sure, than what has occurred in the erection of that portion of the edifice of science with which we are concerned to-day.   It is almost incredible that we should have permitted the present condition of taxonomy to continue.   Why mere tyros, wholly untrained in the underlying principles of the science of classification, should be allowed to contribute to the confusion of taxonomy is a matter which may well make us marvel.   But there have been words of admonition.   Nearly thirty years ago Dr. Gray in his "Botanical Text-book" spoke of the necessity of experience and

"the critical study of the classical botanical works," and then said "No one is competent to describe new plants without such study." Wiser words in regard to the question before us were never written, and had they been heeded during the past quarter of a century we should not have had the present condition of confusion in systematic botany. Certainly our practise of allowing everybody, whether trained for the work or not, to determine the limits of species is taxonomic anarchy.

It is increasingly evident that botanists must insist upon an adequate training by those who are proposing to make and describe new species. Every teacher of botany should impress his pupils with the seriousness of the work of making new species, and should train them to feel that such work should be left to the few who are masters in the subject. The rule which goes into effect to-day, requiring diagnoses of new species to be in Latin, will prove a deterrent to the tyros who would rush into print with their diffuse English descriptions. In this matter, at least, we should all uphold the Vienna code, and rigidly exclude as invalid all publication of species not conforming to it. A more effective deterrent could be provided by an agreement of botanists to restrict publication to certain botanical journals, whose editors should then exercise a revisionary control over all publication of new species. I am well aware of the objection that will be made to such a taxonomic censorship, but we have gone so far in the direction of individual liberty that it has degenerated into license, and some such drastic measure is loudly called for. When we had masters in botany, who were kings to whose authority all must bow, we complained bitterly. Now that the kings are dead the democracy of botany is suffering from the misrule of anarchy. If democracy will not control its subjects we shall have to return to a botanical oligarchy, or even to a dictatorship, for anarchy can not be endured.

Has not the time come for botanists to establish rules

governing and restricting the making of species? I am convinced that the next step forward in systematic botany must be the placing of limitations upon the men who are setting up new species, compelling them to conform their species to the conditions which make species necessary.

Of course this is not the time, nor is it the place, for final action in regard to this matter, and, moreover, I am certainly not the one to formulate rules for species-making, yet I may be allowed to suggest some botanical dicta or aphorisms as a short prodrome of a taxonomic code.

1. Taxonomy is a means, not an end; it does not exist for the taxonomists alone, but for the whole body of botanists.

2. The first purpose of classification is to include all individual plants in as small a number of species as possible.

3. That classification of the plants of the world most fully accomplishes its purpose which gives an adequate picture of the whole in the simplest form.

4. Species have been invented in order that we may refer to great numbers of individuals collectively, instead of singly; therefore the number of species must be far less than the number of individuals.

5. Since we make use of species for the purpose of saving labor in making the acquaintance of plants, it follows that those species whose limitations are so faint or vague that we apprehend them with difficulty have no reason for existence.

6. Scientific classification does not require that every difference in structure and habit be made the basis of a separate species. There must be room left for individual variation, otherwise we should have as many species as there are individual variations.

7. The taxonomist should look for resemblances rather than for differences, so that he may make fewer rather than more species.

8. Species must be so made as to be understood and appreciated by the botanists for whom they are described. A species has no legitimate reason for existence whose limits are perceptible only to its maker.

9. Experience must tell us what limitations of species are most convenient.

10. In making a species the guiding principle must be that it shall be recognizable from its diagnosis. A species that is not distinguishable by its diagnosis has no right to existence.

11. A diagnosis should be brief enough to be remembered readily, for this reason Linné's twelve-word diagnoses are worthy of imitation.

12. Long and complex descriptions should never be used for the limitation of species, and when such long and complex descriptions are found to be necessary this is a sufficient indication that the species should not be made.

These aphorisms are merely illustrative, and by no means cover the whole ground. Others will suggest themselves, especially to those of you who have been engaged in taxonomic work. It seems to me so desirable that a reform in taxonomy should be instituted that I venture to suggest that this society appoint a committee to report upon the feasibility of restoring species to their original importance and dimensions, the possibility of restricting species-making to those who are competent, and also of restricting publication to selected journals, thus involving some kind of taxonomic censorship.

THE TAXONOMIC ASPECT OF THE SPECIES QUESTION

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1. HISTORIC

THE ancients knew and described plants by generic names. Their knowledge of them was general and superficial. According to Adanson,[1] Conrad Gesner, 1559, was the first to indicate the distinction of plants into genera and species, although this advance is also claimed for Columna. Subsequent authors in general, for about a century, arranged species of plants under generic names, but without definite rules for the limitations of genera. Morison (1655), Ray (1682), and Tournefort (1694), defined genera with reference to their fruits and were followed by Linnæus.

Ray regarded specific differences as those that are somewhat notable and fixed and not due to cultivation and which cultivation does not change. The way to determine these, according to him, is to grow them from seed, because all the differences which are found in different plants grown from the same seed are accidental and not specific, but he was not always exact in following this rule.

Tournefort declared that it troubled him very little whether the plants he cited were species or varieties as long as they differed in remarkable and perceptible qualities; Adanson approves this view, remarking that it seems to him sufficient and reasonable.

From Linnæus, Philosophia Botanica, 1751.

We enumerate as many species as different forms were originally created.

[1] Fam. des Plantes 1: 102.   1763.

There are as many species as the Infinite Being originally produced different forms; and these forms, following the laws of reproduction imposed upon them, have produced more, but always similar to themselves. Therefore, there are as many species as there are different forms or structure met with to-day.

From Adanson, Familles des Plantes, 1763.

The moderns define a species of plant as a collection of several individuals which resemble each other perfectly, yet not in everything, but in the essential parts and qualities, without, however, giving attention to the differences caused in these individuals either by sex or accidental varieties.

According to Linnæus (Phil. bot., p. 99) "the species of plants are natural and constant, as their propagation either by seeds or cuttings is only a continuation of the same species. Individuals die, but the species does not."

But we wish to make a distinction between reproduction by seed and that by shoots, offsets, corms, cuttings, suckers or by grafting. These last simply continue the individual from which they are taken and consequently are opposed to the production of new species in plants; *whereas seeds are the source of a prodigious number of varieties, sometimes so changed that they may pass for new species.* He cites, among other examples:

"In 1715 Marchant found in his garden a new species of Mercurialis and the following year it came from self-sown seed; again, four resembled the parent and two were so different that he made another species of Mercurialis. These two new plants were cultivated and continued to grow each year."

It is well known that without foreign fecundation in plants that reproduce by seed, similar changes are induced either by reciprocal fecundation of two different individuals or owing to cultivation, the soil, the climate, dryness or moisture, light or shade, etc. These changes are more or less prompt, more or less durable, disap-

pearing in one generation or perpetuating themselves through several generations, according to the number, the force, the duration of the causes which united to form them, etc., according to the nature, the disposition, the customs, so to speak, of each plant, for it is to be noted that some families do not vary except in the roots, others in the leaves, others in height, pubescence, and color, whereas others change more easily their flowers or their fruit.

It is difficult to define a primitive species and which those are which have originated by successive reproduction or been changed by accidental causes. It is without doubt for this reason that we do not find nowadays a number of plants described by ancient botanists; they have disappeared, either by returning to primitive forms or by changing their form in the multiplication of species. For this reason the ancients knew fewer species; time has brought novelties! And for the same reason future botanists will be *overwhelmed* by the number of species and be obliged to abandon them and be *reduced solely to genera!*

From Lamarck, Encyclopedie Methodique, Vol. 2, 1786.

Species; in botany as in zoology, a species is necessarily constituted of the aggregation of similar individuals which perpetuate themselves, the same, by reproduction. I understand similarity in the essential qualities of the species, because the individuals which constitute it offer frequently accidental differences which give rise to varieties and sometimes sexual differences, which belong however to the same species, as the male and female hemp, in which all the individuals constitute the common cultivated hemp. Thus, without the constant reproduction of similar individuals, there could not exist a true species.

From Rees, Abraham, The Cyclopædia, Vol. XXXIII, 1819.

Species *of Plants,* in *Systematic Botany,* appear, as

far as can be ascertained from the universal experience
of those who are conversant with them, as well as from
everything that can be gathered from the records of
remote antiquity, to remain distinct from each other,
marked by their appropriate characters and qualities,
and renewing themselves periodically by sexual genera-
tion.   Such being the case with all the plants of which
we have any knowledge, we conclude it to be so with the
rest, as well as with animals.   The white blackbird of
Aristotle still inhabits the Cyllenian groves and copses
of Arcadia, undisturbed by the revolutions of two thou-
sand years; and we doubt not that the banks of the
Alpheus have been fringed with the same violets and
primroses, through uncounted ages, as those with which
they are now, every spring, adorned.

Various plants indeed, and especially domestic ones,
like domestic animals, are found liable to some varia-
tions of color, luxuriance, and sensible qualities, which
have led curious inquirers to doubt whether any species
are certainly permanent.   This doubt could arise only
from a slight view of the subject.   Whatever casual
aberrations there may be in the seminal offspring of
cultivated plants, a little observation will prove how
transient such varieties are, and how uniformly their
descendants, if they be capable of producing any, resume
the natural characters of the species to which they belong.

From A. P. DeCandolle and K. Sprengel, Elements of
the Philosophy of Plants, Edinburgh, 1821.

By species we understand a number of plants, which
agree with one another in invariable marks.

In this matter everything depends upon the idea of
invariableness.   When an organ, or a property of it,
is changed neither by difference of soil, of climate, or of
treatment, nor by continued breeding, this organ or prop-
erty is said to be invariable.   When, for instance, we
have remarked during centuries, that the centifolia has
always unarmed leafstalks, we say correctly, that this
property of the centifolia is invariable.

This idea proceeds on the supposition that the species which we know have existed as long as the earth has had its present form. No doubt there were, in the preceding state of our globe, other species of plants, which have now perished, and the remains of which we still find in impressions in shale, slate-clay, and other flœtz rocks. Whether the present species, which often resemble these, have arisen from them; whether the great revolutions on the surface of the earth, which we read in the Book of Nature, contributed to these transitions—we know not. What we know is that from as early a time as the human race has left memorials of its existence upon the earth the separate species of plants have maintained the same properties invariably.

To be sure, we frequently speak of the transitions and crossings of species; and it can not be denied that something of this kind does occur, though without affecting the idea of species which we have proposed. We must, therefore, understand this difference.

We perceive the *Transitions of a Species,* when it loses or changes the properties, which we had considered as invariable in the character. Thus, it would be a transition, if we had stated as an invariable character of winter wheat (*Triticum hybernum*), that it was biennial, and had an ear without awns; and if we should remark, that by frequent reproduction, and by very different treatment, it began to assume awns, and, when sown in spring, came to maturity during the same summer.

But this shows only that our idea of the difference between the two kinds of grains had been incorrect; for it is the universal rule, that the character does not constitute the species, but the species the character. Species, then, only appear to undergo transitions, when we have considered an organ or a property as invariable which is not so.

All properties of plants which are subject to change, form either a subspecies or a variety. By the former we understand such forms as continue indeed during

some reproductions, but at last, by a greater difference of soil, of climate, and of treatment, are either lost or changed. When the different cabbage species receive the same treatment in the same climate, they continue to be frequently reproduced, without changing their appearance. But we can not on this account maintain, that cauliflower would retain the same favorite form in very different climates, and under a complete change of treatment. It at last changes so much, that it can scarcely be distinguished from the common cabbage. This, therefore, is a subspecies. Varieties again do not retain their forms during reproduction. The variable colors —the very variable taste, and other properties of the kitchen vegetables, the ornamental plants, and the fruit-trees, show what varieties are; and the scientific botanist must therefore be particularly attentive to distinguish permanent species from the variable subspecies, degenerate plants and varieties.

To this discrimination belongs, above all things, a careful, continued, and unprejudiced observation of the whole vegetation of the same plant during its different ages, and amidst the most different circumstances which have an influence on it. When, for instance, in the common *Lotus corniculatus,* on whatever soil it may grow, we uniformly observe that it has a solid stem, even and erect divisions of the calyx, and expanded filaments, we must of necessity distinguish, as a particular species from it, another form which grows in bogs and in watery meadows, which has a much higher, and always hollow stalk, the divisions of its calyx spread out into a star-shape and hairy, and which has uniformly thin filaments; and we must name this latter species either *Lotus uliginosus* with Schkuhr, or *Lotus major* with Scopoli and Smith. As, on the other hand, the *Pimpinella Saxifraga* grows sometimes quite smooth, and sometimes in woods and shady meadows, considerably hairy; as it displays sometimes simple and small stem-leaves, sometimes half and even doubly pinnated leaves; and as these

forms vary according to the situation of the plant and
during reproduction, we can not regard these forms by
any means as distinct species, but we must view them as
corruptions.

We see, that, in order to decide respecting the idea of
a species, an observation of many years, and of much
accuracy, is often required; and that the cultivation of
plants, from the most different climates, in botanical
gardens, is in the highest degree necessary for their dis-
crimination.

From Lindley, John, An Introduction to Botany, Lon-
don, 1832.

A *species* is a union of individuals agreeing with each
other in all essential characters of vegetation and fructi-
fication, capable of reproduction by seed without change,
breeding freely together, and producing perfect seed
from which a fertile progeny can be reared.   Such are
the true limits of a species; and if it were possible to
try all plants by such a test, there would be no difficulty
in fixing them, and determining what is species and what
is variety.   But, unfortunately, such is not the case.
The manner in which individuals agree in their external
characters is the only guide which can be followed in the
greater part of plants.   We do not often possess the
means of ascertaining what the effect of sowing their
seed or mixing the pollen of individuals would be; and,
consequently, this test, which is the only sure one, is, in
practice, seldom capable of being applied.   The deter-
mination of what is a species, and what a variety, be-
comes therefore wholly dependent upon external char-
acters, the power of duly appreciating which, as indic-
ative of specific difference, is only to be obtained by ex-
perience, and is, in all cases, to a certain degree arbitrary.
It is probable that, in the beginning, species only were
formed; and that they have, since the creation, sported
into varieties, by which the limits of the species them-
selves have now become greatly confounded.   For ex-

ample, it may be supposed that a rose, or a few species
of rose, were originally created.   In the course of time
these have produced endless varieties, some of which,
depending for a long series of ages upon permanent
peculiarities of soil or climate, have been in a manner
fixed, acquiring a constitution and physiognomy of their
own.   Such supposed varieties have again intermixed
with each other, producing other forms, and so the opera-
tion has proceeded.   But as it is impossible, at the
present day, to determine which was the original or orig-
inals, from which all the roses of our own time have
proceeded, or even whether they were produced in the
manner I have assumed; and as the forms into which
they divide are so peculiar as to render a classification
of them indispensable to accuracy of language; it has
become necessary to give names to certain of those forms,
which are called species.   Thus it seems that there are
two sorts of species: the one, called natural species, de-
termined by the definition given above; and the other,
called botanical species, depending only upon the ex-
ternal character of the plant.   The former have been
ascertained to a very limited extent; of the latter nearly
the whole of systematic botany consists.   In this sense
a species may be defined to be ''an assemblage of indi-
viduals agreeing in all the essential characters of vegeta-
tion and fructification.''   Here the whole question lies
with the word essential.   What is an essential character
of a species?   This will generally depend upon a prone-
ness to vary, or to be constant in particular characters,
so that one class of characters may be essential in one
genus, another class in another genus; and these points
can be only determined by experience.   Thus, in the
genus Dahlia, the form of the leaves is found to be sub-
ject to great variation; the same species producing from
seed, individuals, the form of whose leaves vary in a
very striking manner; the form of the leaves is, there-
fore, in Dahlia, not a specific character.   In like manner,
in Rosa, the number of prickles, the surface of the fruit,

or the surface of their leaves, and their serratures, are found to be generally fluctuating characters, and can not often be taken as essential to species. The determination of species is, therefore, in all respects, arbitrary, and must depend upon the discretion or experience of the botanist.

From Nicholson, Henry Alleyne, A Manual of Zoology, New York, 1876.

Species.—No term is more difficult to define than "species," and on no point are zoologists more divided than as to what should be understood by this word. Naturalists, in fact, are not yet agreed as to whether the term species expresses a real and permanent distinction, or whether it is to be regarded merely as a convenient, but not immutable, abstraction, the employment of which is necessitated by the requirements of classification.

By Buffon, "species" is defined as "a constant succession of individuals similar to and capable of reproducing each other."

DeCandolle defines species as an assemblage of all those individuals which resemble each other more than they do others, and are able to reproduce their like, doing so by the generative process, and in such a manner that they may be supposed by analogy to have all descended from a single being or a single pair.

M. de Quatrefages defines species as "an assemblage of individuals, more or less resembling one another, which are descended, or may be regarded as being descended, from a single primitive pair by an uninterrupted succession of families."

Müller defines species as "a living form, represented by individual beings, which reappears in the product of generation with certain invariable characters, and is constantly reproduced by the generative act of similar individuals."

According to Woodward, "all the specimens, or individuals, which are so much alike that we may reasonably

believe them to have descended from a common stock, constitute a *species*."

From the above definitions it will be at once evident that there are two leading ideas in the minds of zoologists when they employ the term species; one of these being a certain amount of resemblance between individuals, and the other being the proof that the individuals so resembling each other have descended from a single pair, or from pairs exactly similar to one another. The characters in which individuals must resemble one another in order to entitle them to be grouped in a separate species, according to Agassiz, "are only those determining size, proportion, color, habits and relations to surrounding circumstances and external objects."

On a closer examination, however, it will be found that these two leading ideas in the definition of species—external resemblance and community of descent—are both defective, and liable to break down if rigidly applied. Thus, there are in nature no assemblages of plants or animals, usually grouped together into a single species, the individuals of which *exactly* resemble one another in every point. Every naturalist is compelled to admit that the individuals which compose any so-called species, whether of plants or of animals, differ from one another to a greater or less extent, and in respects which may be regarded as more or less important. The existence of such individual differences is attested by the universal employment of the terms "varieties" and "races." Thus a "variety" comprises all those individuals which possess some distinctive peculiarity in common, but do not differ in other respects from another set of individuals sufficiently to entitle them to take rank as a separate species. A "race," again, is simply a permanent or "perpetuated" variety. The question, however, is this —How far may these differences amongst individuals obtain without necessitating their being placed in a separate species? In other words: How great is the amount of individual difference which is to be considered

as merely *"varietal,"* and at what exact point do these
differences become of *"specific"* value? To this ques-
tion no answer can be given, since it depends entirely
upon the weight which different naturalists would attach
to any given individual difference.[2] Distinctions which
appear to one observer as sufficiently great to entitle the
individuals possessing them to be grouped as a distinct
species, by another are looked upon as simply of varietal
value; and, in the nature of the case, it seems impossible
to lay down any definite rules. To such an extent do
individual differences sometimes exist in particular
genera—termed "protean" or "polymorphic" genera—
that the determination of the different species and vari-
eties becomes an almost hopeless task.

The second point in the definition of species—namely,
community of descent—is hardly in a more satisfactory
condition, since the descent of any given series of indi-
viduals from a single pair, or from pairs exactly similar
to one another, is at best but a probability, and is in no
case capable of proof.

Upon the whole, then, it seems in the meanwhile safest
to adopt a definition of species which implies no theory,
and does not include the belief that the term necessarily
expresses a fixed and permanent quantity. Species,
therefore, may be defined as *an assemblage of individuals
which resemble each other in their essential characters,
are able, directly or indirectly, to produce fertile indi-
viduals, and which do not (as far as human observation
goes) give rise to individuals which vary from the gen-
eral type through more than certain definite limits.* The
production of occasional monstrosities does not, of
course, invalidate this definition.

From Gray, Asa, Structural Botany, Ed. 6, 1879.

Species in biological natural history is a chain or series

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[2] As an example of this, it is sufficient to allude to the fact that hardly
any two botanists agree as to the number of species of willows and
brambles in the British Isles. What one observer classes as mere varieties,
another regards as good and distinct species.

of organisms of which the links or component individuals are parent and offspring. Objectively, a species is the totality of beings which have come from one stock, in virtue of that most general fact that likeness is transmitted from parent to progeny. Among the many definitions, that of A. L. Jussieu is one of the briefest and best, since it expresses the fundamental conception of a species, *i. e.*, the perennial succession of similar individuals perpetuated by generation.

The two elements of species are: (1) community of origin; and, (2) similarity of the component individuals. But the degree of similarity is variable, and the fact of genetic relationship can seldom be established by observation or historical evidence. It is from the likeness that the naturalist ordinarily decides that such and such individuals belong to one species. Still the likeness is a consequence of the genetic relationship; so that the latter is the real foundation of species.

No two individuals are exactly alike; and offspring of the same stock may differ (or in their progeny may come to differ) strikingly in some particulars. So two or more forms which would have been regarded as wholly distinct are sometimes proved to be of one species by evidence of their common origin, or more commonly are inferred to be so from the observation of a series of intermediate forms which bridge over the differences. Only observation can inform us how much difference is compatible with a common origin. The general result of observation is that plants and animals breed true from generation to generation within certain somewhat indeterminate limits of variation; that those individuals which resemble each other within such limits interbreed freely, while those with wider differences do not. Hence, on the one hand, the naturalist recognizes *varieties* or differences within the species, and on the other *genera* and other superior associations, indicative of remoter relationship of the species themselves.

From Darwin, Origin of Species, new edition, from the
sixth English edition, New York, p. 33, 1883.

No one definition has satisfied all naturalists; yet every
naturalist knows vaguely what he means when he speaks
of a species. . . . The term variety is almost equally
difficult to define; but here community of descent is
almost universally implied, though it can rarely be
proved.

From Britton and Brown, Illustrated Flora 1: VI., 1896.

A species is composed of all the individuals of a kind
capable of continuous successive propagation among
themselves.

From De Vries, Species and Varieties, p. 32, 1905, under
Elementary Species in Nature.

"What are species?" Species are considered as the
true units of nature by the vast majority of biologists.
They have gained this high rank in our estimation prin-
cipally through the influence of Linnæus.   They have
supplanted the genera which were the accepted units
before Linnæus.   They are now to be replaced, in their
turn, by smaller types, for reasons which do not rest
upon comparative studies but upon direct experimental
evidence.

2.   DISCUSSION

Any method of evolution makes difficult the establish-
ment as a general conclusion, that all the progeny of a
species must belong to that species.   The paleontologists
have always faced this difficulty; their species have of
necessity been assumptions, and theoretically, at least,
if the complete representation of any line of descent
could be assembled it would be seen at once that the
whole series of forms were in some way connected.   The
induced mutation effected by MacDougal in *Raimannia
odorata,* in which plants so different from their imme-
diate parent as to appear, at least, specifically distinct

from it, as compared with other feral species, is a notable addition to the difficulty of maintaining such a conclusion.

As long as species were generally understood to be relatively fixed in characters, their delimitation was relatively simple, but the general understanding that all living organisms are descended from others which were different from them has greatly complicated the subject.

Whether the evolution has been by imperceptible progressive modifications of structure, or by mutations, or by both methods, the result is essentially the same from the practical standpoints of taxonomy; from these standpoints, then, similarity of individuals must remain the consideration to which most weight will be given in taxonomic usage. It has been conclusively proved that many mutants and elementary species or races breed true in enough instances to establish the rule for at least a number of generations; this should not, however, in my opinion, admit them to the category of species, which, though necessarily difficult in delimitation, will still remain the practical taxonomic groups, recognizing, nevertheless, that they are made up of either relatively constant or of widely fluctuating elementary components, which, in turn, will presumably yield the species of future geologic ages.

The recognition of the existence of incipient or elementary species or races within the composition of species, explains, in large part, the multiplication of species and of groups of assumed lower rank, in many of the larger genera, nearly every taxonomist, except the most conservative, having taken more or less part in thus increasing the number of descriptions and of names. They have been variously denominated species, subspecies, varieties, subvarieties and forms, according to the point of view of the investigator.

Geographic distribution has been invoked as a very useful aid in determining the limits of species. It is a well-recognized fact that certain areas of the earth's surface, some large, some small, are characterized by types

of plants which differ from those of other areas, either contiguous or widely separated, and, in cases where types inhabiting different areas so characterized are apparently similar, though different, their separation or isolation has been given weight in regarding them as specifically distinct.   No doubt this is a rational course to pursue if it is not carried to extremes.   The question whether the environments to which the ancestors of such types have been exposed have been the cause of their differentiation, or whether the elementary species have been perpetuated which were best adapted to the soil, climate or other features of the environments, is one of the most interesting of unsolved problems.   That similar types have for the most part come from common ancestors we must regard as most probable, even if now inhabiting widely separated regions, segregated by the disappearance of related types in intervening space, being thus remnants of the more general distribution of the ancestral forms in earlier geologic eras.

Geographic distribution must, however, in cases of contiguous land districts, be cautiously used as a determining factor.   There are many instances in which a species with certain well-marked characters in one region is, apparently, at least, completely connected through intermediate characters with what is readily regarded as a perfectly distinct species in another region.   Instances of this kind are within the experience of every one who has given attention to geographic distribution of plants. I say this is apparently the case; the conclusion is based on long series of herbarium specimens and on field observations made over large areas of country.   Neither of these methods of information is wholly satisfactory, because the herbarium series must necessarily be limited in the number of specimens, and also because the field observations have to be taken at different times and usually at widely separated intervals.   Still, the consensus of opinion of plant geographers leans strongly to the existence of intermediate forms in intermediate regions.

Some of these are almost certainly hybrids, but it would not be safe for us to conclude that they all are. Some light has been thrown on this question by the growing of the extreme forms side by side, and more information can doubtless be thus obtained, the principal difficulty being that the environment of the one is often fatal to the other. A better method would be to grow the two apparent extremes within the natural environment of the apparent intermediates.

3. The Taxonomic Treatment of Groups assumed to be of Lower Rank than Species

There is perhaps no taxonomic subject on which greater diversity of opinion and practise exists than in the arrangement and nomenclature of groups of individuals not accorded full specific value. The relationships of these groups to the group assumed to constitute the species proper, and the nomenclature of these subsidiary groups, vary all the way from regarding them all as species, to regarding some of them as subspecies, some as varieties, some as subvarieties, others as forms, while even finer distinctions have been attempted, and elaborate monographs of many genera have been written in the attempt to express descriptively these interrelationships. It has been very evident that these described groups are of unequal value, some resembling the assumed typical group more, some less, and in a good many instances very little. The general result of these attempts to dissect nature has been embarrassing, because when a subsequent student takes up the group he is wholly unable to determine from any descriptions that can be written where any given individual would have been grouped by the previous author, unless he has access to the actual specimens which the previous author studied, and the subsequent student also finds that the examination of a large number of different individual specimens from those studied by his predecessor contains some which

do not fully agree with any one of his predecessor's descriptions, or he finds that some of his specimens agree about as well with one of the groups recognized by the previous author as they do with another. This result shows conclusively that for practical taxonomic purposes it is not desirable to attempt to define a great many of these minor groups. The tendency has been brought about, I believe, by the instinct of many investigators that everything in nature must be named and described, but nothing is to be gained by permitting this laudable purpose to run to extremes.

It is evident, I think, that our taxonomy has been based on the fundamental error that the plant world is to be regarded as divisible into smaller and smaller groups, rather than following nature and proceeding on the theory that it is built up of greater and greater ones; the science should be synthetic rather than analytic. The synthetic theory will give our observation and experimentation a different significance and enable us to comprehend some of the phenomena now masked by the analytic method of attack.

If, as now seems more probable than a few years ago, species are made up of elementary species, or races, and that these are being increased by mutation, there can be no end to the number of such groups produced. As to the designation of these groups, I suggest that the term race be employed. This has long been used to designate what have been called self-perpetuating varieties, which appear to me to be identical with the present conception of elementary species, and its application may readily be widened. The term variety loses its significance, because it is usually quite impossible to tell how any given individual or group of individuals has arisen, or from which species it has sprung. The term form could be used instead of either race or elementary species, but it has had such a trivial significance in literature that race seems to be preferable. Subspecies implies divisibility, and is, therefore, an undesirable term.

In conclusion, I submit the following propositions:

1. The individual is the taxonomic unit, usually un-designated.

2. Similar individuals constitute a race.

For general taxonomic purposes races need not be designated; the conception and description of the species is broad enough to include all races of which it is composed. There will never be complete uniformity of agreement as to the distinction between races and species, any more than there will ever be complete agreement as to the limitations of genera. It is futile in science to attempt to lay down principles which interfere with individual judgments. For special purposes the races may be designated numerically, as, *Quercus alba,* race 2; *Œnothera biennis,* race 12; *Bursa Bursa-pastoris,* race 17; *Draba verna,* race 104. There are doubtless many instances where the species is composed of only one race, just as we have monotypic genera composed of but one species.

3. Similar races constitute a species, the species designated binomially.

4. Similar species constitute a genus, the genus designated monomially.

THE PHYSIOLOGIC ASPECT OF THE SPECIES QUESTION

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NOT being sure of what ground might already be covered by the speakers who have preceded me on the program, I take the liberty of presenting my matter after giving thought to what has been said; and I find in mentally reviewing this—that the species concept as presented by the previous speakers does not embrace the whole field as it is forced upon me in my every-day work. I am especially surprised at this, because the first speaker, under whom I secured my elementary training in botany, is very particular in giving instruction to his pupils to begin with the one-cell plant and to work up from the simple to the complex. Yet, so far as I could ascertain in listening most carefully, he has not now taken into consideration a single one of the simple plants of which he knows there are many thousand times as many as there are of flowering plants, therefore I seem to be left somewhat adrift for my presentation.

I will not attempt to give any historical aspect of the question, but to take it up from the point in which it appeals to me in my every-day work, for it is a problem that I have been obliged to meet, and as I have met it, I will present the results to you.

As I understand it, we are taking up the question of the species concept. I thought it quite well worth while, in looking up the matter, to see what a man who has entirely changed the aspect of the subject within not so very many years might say as to what he considered a species concept, and so I very carefully again looked through my copy of Darwin's "Origin of Species." If

a man were going to revolutionize the world of thought he certainly, I assumed, would give a definition of the subject he is going to treat. But I could not find a word as to what Darwin meant by species. He writes as if all the world knew what species are. Yet I did find this in the latter part of the last chapter; he says, "And now we shall be freed from the vain search for the undiscovered and undiscoverable essence of the term species." Consequently, here we are, tracing a will-o'-the-wisp. And yet, it seems to me, there must be something that we are all thinking about when we say species. There must be some workable idea. Of course I know that since Darwin's time and the vast accumulation of knowledge in reference to heredity and variation, to say nothing about other physiological aspects proper, our ideas have decidedly changed. Still, as I look over the actual work being accomplished in determining the number and the extent of the species of plants in the world, I do not see that our practise especially differs from the pre-Darwinian practise. We have a theoretical idea of what species are, but practically we describe them for the most part in the same pre-Darwinian terms, the really Linnean terms, so far as many of us can, although we do not adhere to the Linnean brevity. Nevertheless, there are some instances in which it seems necessary to deviate from this practise, if we wish to handle our subject in such a way as to make it useful; for I assume, in the first place, that whatever the species concept may be, it is something which enables us to present ideas or problems in a better form than we could otherwise accomplish. At any rate, the idea of a species is a mental tool of some sort.

To take up the purely physiological aspect; possibly it was the study of bacteria which forced this phase of the question upon us for the first time. I judge that it came largely from the fact that bacteria are so very minute. What could one do if he were going to describe the thousands of species of bacteria simply as plants,

with genera and life history as in the case of other plants? In the first place, morphological characters are too ill-defined, if indeed they exist, and so he was forced to devise some other means of discrimination. This means was at first almost purely physiological. It largely depended upon the behavior of the individual sorts, or the groups of individual sorts, to certain nutritive processes. It depended upon what kind of media the bacteria grow upon, the temperature, and access to oxygen. Upon these physiological results in large part have been built our vast knowledge, economic very largely, of the many kinds of bacteria which are designated as species. But we may pass by the bacteria for a time and take up the larger organisms. I think the ones that are most useful in this connection are the strictly parasitic forms.

There is no more interesting and better understood group at the present time than the plant-rusts. The forms are sufficiently large to furnish a variety of species and genera exhibiting morphological characters, and yet, being strictly parasitic, are particularly restricted by the nature of the substratum. I will give one or two instances to illustrate. There is a group of forms—I will admit that I hardly know what terms to use in speaking of them, but I will say a group of forms—which grow upon the various species of Carex. It is found that by taking rust spores from a single host of any particular Carex and sowing them upon an Aster, or a Solidago or an Erigeron, they will grow upon one of these genera, it makes not much difference what the species, but not upon the other two. Now if spores are taken from another Carex, the spores being so exactly like the former that they can not be distinguished by any visible characters, and sown upon plants of the same three genera, they may grow upon a different one than in the former instance, but not upon the remaining two. Thus finally we will get three sets of forms, one growing on Aster, one on Solidago and one on Erigeron, which can not be

made to interchange, although they possess no evident morphological differences. This result depends, as I assume and as seems to be pretty well authenticated by all the researches, upon a question of nutrition. It does not depend upon any peculiar structure of Aster, Solidago or Erigeron; but here we have three genera which furnish different kinds of nutritive matter, or in some way differently affect the nutrition of the fungus, so that a fungus which has adapted itself to live upon one of these generic groups of plants will not live upon, or can not live upon, the other. It is a very nice adjustment to a particular kind of nutriment; I think we are quite well assured of that fact.

Now, the question arises, are these three species? If you choose to look up the literature, you will see that the speaker has described them as three species under three independent names. That does not mean that he believes they are truly three species, but that it was a convenient way of designating the three physiologically different kinds until a time when the matter could be more fully considered. Now, are these three species? Well, to confess to you, not to say it too loudly, I do not believe they are. They are not three species in the generally accepted sense because they can not be distinguished morphologically. What then is, or should be, our conception of a species? Is it something to be distinguished physiologically or morphologically, or in both ways? This is not a hypothetical question, because the literature of the subject that I represent is very full of descriptions of species based entirely or partially upon physiological data, and I am assured that we are not alone in this method of describing species.

If I understand aright, the ornithologists, at least some of them, are willing to assert that species may differ by characters which can not be described by words [laughter]; that is to say, you will know the species when you see it, but you can not describe it in any language by which another person may recognize it. I

think that this is not a joke, but that it is really stated
in earnest; because, I read it in *Science*.   [Laughter.]
But I fancy botanists have not gone quite that far.

Now, just another instance that arose during an ex-
tensive series of culture studies; that is the case of the
Helianthus rusts.   They have been described according
to the host plants on which they grow.   Each species
of Helianthus and its close relatives appear to bear
a distinct kind of rust, which acts in cultures as if it
were an independent species.   Yet any and all of these
will grow on Helianthus annuus, a so-called bridging
host.   Are these different species different biological or
physiological species, or simply forms or races?   Pos-
sibly it would be well to refer them to some sub-category,
as Dr. Britton has suggested.

I think when we come to study other parasitic forms
thoroughly we shall find this condition equally true, for
instance, in the genus Cuscuta among flowering plants.
Furthermore it is probably true in many cases of plants
which are not parasitic.   We had an illustration this
morning in the cultures of Penicillium exhibited by Dr.
Thom, where characters of taxonomic importance were
developed according to the medium on which the fungus
was grown.

It seems highly probable that a physiological cause
for variation, which may be considered as specific under
many circumstances, could be traced throughout the
vegetable kingdom.   For purposes of study I assume
that in most cases of physiological species, they may
develop in the course of time into true taxonomic species,
having distinct morphological characters, and that in
cases such as I have enumerated, we are dealing with
nascent species.   The rules which have been laid down
in the presentation of the subject by the previous
speakers apply more particularly, I think, to forms well
differentiated morphologically.   But due recognition
should be given to forms of physiological origin, as I
have shown.   Finally, I would say, at least it is a rule

which I have formulated for my own guidance—it was a necessity that I should formulate some rule—that species, which are concepts, as I take it, for our convenience in discussing the various questions pertaining to plants, should be distinguished by sufficient morphological characters, the distinctions based upon physiological differences having subspecific rank.   What constitute sufficient morphological characters must be left to the individual judgment.

THE PHYSIOLOGICAL ASPECT OF A SPECIES

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THE simple recognition of different kinds of plants must be of great antiquity, and perhaps no single idea affords a better index of scientific thought during the last few centuries than the species conception. The occasion does not warrant a detailed statement of its development farther back than the time of Linnæus, who gave the idea a distinctly morphological stamp which it has retained to the present day. His systematization of natural objects marked the beginning of a period in which the morphological view of nature has prevailed throughout, the mechanics of form reaching its very apotheosis in the writing of De Candolle, De Bary, Hofmeister, Schwendener and a score of other eminent investigators who have triangulated the field of natural history of plants, basing relationships and constructing systems of phylogeny upon pure form, and upon the mechanical relations of cell-structure.

A century since, the ideas of continuing origination and endless evolutionary change took on definiteness and clearness with the writings of Lamarck, and this has grown until a distinctly vitalistic and genetic view-point has been gained, with the inevitable rearrangement of perspectives and modifications of conclusions as to the groupings and manner of relationships among living things.

Latterly, after statistical methods had reached a state of fair efficiency, their introduction into the study of occurrence, characters, distribution and form, has resulted in leading consideration from the type or the individual, to aggregates, or to the whole mass of individuals

of a group, by which amplitude of variation and mode of ontogenetic procedure may be accurately outlined.

The development of this aspect of natural history has been followed by a truer estimation of capacities and activities as attributes of organisms, with the result that even morphology has come to be based upon physiological principles, upon which alone it may make further material progress.

The groups with which the physiologist deals in the detection of activities, estimations of functions and measurements of performance, consist of a series of generations of individuals through which identical qualities, characters and capacities are transmitted uniformly within the limits of fluctuating variability. These groups may sustain the most diverse relationship and all possible degrees of affinity, but differ essentially in their physiological response to any given environment under permanent existence in it.

To test such conceptions of hereditary entities implies pedigreed cultures, or observations upon lineal series under known conditions of descent, hybridization operations and statistical estimations. The various qualities do not display themselves equally throughout the metameres of the sporophyte, and it is by no means to be assumed that the flower, or the terminal portion of the shoot surviving at maturity, is a compendium of the various developmental stages. Nowhere is this more beautifully apparent than in intermediate hybrids of the first generation, in which the qualities of one parent predominate in the leaves and the other organs of the first, or lower internodes, while those displayed by the upper terminal portions of the stem and flowers may be those of the other parent. Exemplifications of this fact have also been observed, in which the internodes and the organs formed during the first season's growth in two nearly related forms were widely different, displaying divergent structures and different "nasties" and tropisms. During the second year's growth, the organs formed

would be so nearly alike as to be in themselves inadequate for the separation of the two by ordinary taxonomic methods. These facts, which have been illustrated more than once in my own cultures, are quite at variance with the supposition that closely related forms are most alike in the seedling and younger stages and most divergent in the members of the adult formed latest.

Another form of transgressive variability is found when some descendants of individuals belonging to strain A, are apparently but little separated from B. Morphologically this would appear as an intergradation, but in reality the resembling individuals are divided and divisible into two groups, each carrying its own inherited potentialities, and in their progeny arranging themselves more or less symmetrically around the form of the strain, race or species. That the inclusion of the two is widely different may be illustrated in a striking manner by their action when crossed by a third form.

It can not be maintained that taxonomic thought has accurately or quickly reflected these modern estimations of the nature of living forms, for the very magnitude of the system necessary for the expression of relationships operates to prevent anything like a rapid or accurate adjustment.

Taxonomy is an eminently practical phase of botany, and it may reach its greatest general and total usefulness by confining its practise to the delineation of readily appreciable entities whether they be "natural" or "artificial."

So far as investigation in genetics and in the general functional activities of plants is concerned, however, progress is to be made only by increasing precision of measurement, and refined exactness of method of estimation of the qualities and characters concerned in the activities of the organism in both heredity and functional performance. The realization of this requirement comes but slowly. There are writers who still insist that the intricate pattern woven by the plant during its ontogeny,

as determined by micrometric measurements, developmental observations, experimental tests and statistical estimations upon the aggregate of the group, shall be capable of demonstrations by the foot rule and hand lens applied to the apical structures exhibited by a single individual of the mature sporophyte, as if the pedometer and hand compass were adequate for testing the results of a triangulation made by the transit and steel tape. In other words, botanists of academic habit will with the greatest gravity attempt to read out of existence, and estimate of no importance, hereditary groups of organisms unless they conform to certain illy defined arbitrary standards.

Taxonomic thought rounds its broadest conceptions when its conclusions are based upon the aggregate of individuals within natural groups, and embody ontogenetic procedure, environmental relations, heredity, evolutionary change and comparative functional performance. So organized it might rightly lay claim to being ''philosophical botany,'' and would include an orderly arrangement of all knowledge of plants, and would form the basis upon which all researches might be founded.

Taxonomic practise is quite another matter; hampered as it is by an outworn and mediæval method of giving names to living organisms, it is doubtful as to how far we might demand of it that it discriminate among the many degrees of relationship which reveal themselves in capacities and performance as well as in refinements of form. The more thoroughly and accurately however, that it takes into account the total sum of the attributes, qualities and capacities of the plant, the greater will be the value of its conclusions, and the greater will be the service it may render to coordinate branches of botanical science.

AN ECOLOGIC VIEW OF THE SPECIES CONCEPTION

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I. PAST AND PRESENT PRACTISE IN SPECIES-MAKING

THE species may be either a means or an end; properly it is both. In descriptive botany, these two uses of the species have often been confused. The describing of new species has come to be recognized as an end in itself, while it should be nothing more than a necessary preliminary to further and more important botanical study. The interest of the ecologist in the proper recognition and naming of species is necessarily greater than that of nearly all other botanists. To him species are an indispensable means in the study of vegetation. On the other hand, the search for the definite results of adaptation and evolution, which is his final work, leads him inevitably to the species as an end. It is this double significance of the species for the ecologist that makes him peculiarly concerned about its treatment. So long as he uses the species only as a means, he is not greatly confused, except as a consequence of the fact that species are habitually made in the herbarium upon a small number of specimens, while he meets them as hundreds and thousands of variable individuals. His serious troubles begin with experimental work in adaptation and evolution. It quickly becomes evident that species so-called are widely different in rank, origin and relationship. Some are clearly species in the usual sense, while others are merely variations and forms of these. The ecologist thus comes to look with doubt upon all species. He accepts them reluctantly and provisionally until they meet successfully the test of experiment.

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Even a casual survey of the practises in species-making during a century or more shows little or no uniformity of criteria or results.   A comparison of methods in the different plant groups is even more striking.   This lack of uniformity is found not only in the work of botanists in general, but even in the work of the same botanist.   The consequences in the form of unequal and invalid species have been almost innumerable.   This is particularly true of the fungi.   To one familiar with them, it seems certain that the number of valid species is considerably less than half the number published.   Attempts to guide the descriptive botanists and to make species more definite and uniform have not been wanting.   A few of these have been noted, in order to show how little effect they had, even upon their own authors, and how utterly impossible of application they are without the test of experiment.

The criteria proposed by Ray were permanence of form and appearance, and non-fertility with other species. This appears to be little more than an attempt to justify the practise prevalent under the dogma of special creation.   Mere observation could give little support to either criterion, and the thought of experimental support was scarcely dreamed of.   As a pioneer in evolution, Lamarck gave a definition of the species, which would be expected to warrant more than passing interest.   He defined a species as a ''collection of similar individuals which are perpetuated in the same conditions as long as their environment is not changed sufficiently to bring about variation in their habits, their character or their form.''   It is clear that the whole value of this definition depends upon the significance given to the word variation.   Lamarck, in his strong feeling for adaptation, hit upon the two essential facts, environment and variation, but his application of these criteria was purely academic.

It is a significant fact that Darwin should have written the '' Origin of Species'' without pointing out just what he meant by a species.   His task was to prove origin

by descent as opposed to origin by special creation. For this purpose, it was unnecessary as well as impossible to define a species or to discover the method by which it originates. Darwin regularly used the terms species, subspecies and variety, but he did not draw a definite and constant line between them. De Vries has taken the first definite step in advance by the use of experiment to determine a species. It remains to be seen whether his concept of elementary species will clarify or confuse. It can not be accepted even provisionally until much more experimental work has been done.

In the last decade or two, conservative American botanists have often expressed the view that proper specific characters can be drawn only from the flower and fruit, or from the reproductive parts, whatever they may be. Since this has sometimes been said to have been Dr. Gray's view also, it seemed that it would be both profitable and interesting to compare the criteria of conservative and radical describers of species in the same family and genus. Time was lacking for a thorough and complete comparison, but in the few families selected the results seem representative. It was quickly seen that many current species accepted by all were not based upon reproductive characters, and that some of the most doubtful of recent ones were. It further appeared that, while habit, leaf, stem, etc., played slightly more important parts in later work, there was little essential difference in the kind of criteria used. The striking difference lay in the fact that the new species segregated are based upon much smaller variations of the parts concerned, as a rule, and are consequently much more difficult to distinguish when represented by many individuals.

The ecologist finds it a necessity to be able to distinguish and to refer to any difference represented by a number of individuals. A form or a variation is just as important to him as a species, and often presents a better point of attack. He must consequently be partly in sympathy with the present tendency of descriptive bot-

any to search out and describe all groups that are different, regardless of the degree of difference. He must, however, know the relationship of these groups, *i. e.*, whether they are coordinate species, forms or what not. To publish them all as binomials regardless of their rank completely hides their relationship to species already in existence. It is easy to understand that this has resulted partly from the fact that a trinomial is longer and hence less convenient than a binomial. Convenience is much less essential than accuracy and clearness, and must eventually yield to permit the regular use of the trinomial to designate the various differentiations of a species. The treatment of all groups below the genus as essentially coordinate is due even more to the fact that questions of ancestry and of origin enter all too rarely into the making of new species. These are questions that can be settled only by the most extensive and intensive field work, followed by thorough experiment. For such work there has as yet been almost no time or sympathy, as is shown by the all but hopeless mélange of so-called new species.

II. Bases for Distinguishing Species

The universal basis for distinguishing species has been the degree of morphologic difference. Physiologic and ecologic differences have but rarely been taken into account, except in such groups as the bacteria. The morphologic treatment is based upon the fundamental fact that stable structures are ancestral, and plastic ones derived. This has led to the basic principle that reproductive characters are of greater worth than vegetative ones. With this the ecologist is in full accord theoretically, but he would wish to have experimental evidence before accepting it as universally true. In fact some of the little evidence at present available indicates that this rule must permit some exceptions. It must constantly be borne in mind, especially by those who believe that evolution is always a question of the germ-plasm, that

vegetative features alone are present in the blue-green algæ and many of the fungi. It is evident that the method of morphologic differences greatly facilitates the provisional cataloguing of a flora, but it suffers from a universal and serious fault. This is the use of a few herbarium specimens in lieu of a large number of field individuals. Practically every collector selects a few individuals that appear typical, while for the purpose of scientific species-making he should collect as complete a series as possible of divergent individuals. Even if this were done, the ecologist must continue to regard the method as a mere preliminary, which serves to arrange the material and hence to facilitate the real study of species.

Closely connected with morphologic difference is the question of the absence of intermediate forms. This appears to have played a more important part in zoology than in botany. In the latter case, at least, it seems often to have been taken for granted as a necessary consequence of structural differences. At best, it has regularly been a question of intermediate forms in the herbaria and not in the field.

Constancy as a criterion of species is also but another phase of morphologic difference. As such it seems to have been used chiefly to designate uniformity of difference throughout the individuals concerned. The constancy of a structure from one generation to another, or from one habitat to another has been given little attention in species-making. Yet it is precisely these which are of fundamental importance. This fact, however, makes it at once evident that constancy is something that can only be determined by combining the most extensive field observations year after year with experiments in various habitats. This makes it clear that our present knowledge of constancy is almost purely theoretical, and that it is profitless to discuss it in our present ignorance of it.

To the ecologist, then, the usual bases for distinguish-

ing species, viz., degree of morphologic difference, absence of intermediate forms, and constancy, are entirely inadequate.   He sees three critical facts in the development of a new species or any new form: (1) ancestry, (2) habitat or method of origin, (3) structural changes, very rarely functional ones.   None of these can be studied adequately anywhere but on the ground.   The first two are purely experimental questions.   While the most thorough field study is a necessary preparation for them, they can never be decided except by experimental methods in the field.   Apart from the study of the origin and structure of vegetation, the fundamental task of the ecologist is the experimental investigation of the origin of new forms, the so-called species.

III.   Ecologic Procedure

The questions of what a species is, what are species and what are not, and of the origin of species and of forms must then be decided by experiment.   The method of attack is easily determined, but the procedure is superlatively slow and laborious, and the demand upon time and patience unlimited.   In spite of his inclination, the ecologist finds it necessary to accept as a working basis the species at present distinguished.   His first task is to discover those that seem to give the best promise of results under experiment.   The procedure consists of two essential processes: (1) field observations throughout the habitat of the species concerned and (2) experiment.   The latter is the crux of the whole question.   It consists of three steps: (1) the exact measurement by instruments of the original habitat and the new one, (2) the experiment itself and (3) the measurement of results, *i. e.*, the determination of the degree of morphologic and histologic difference.   The detailed procedure in each of these has been given in ''Research Methods in Ecology''[1] and it is unnecessary to repeat it here.   It is sufficient to indicate that experiment should proceed whenever possible

[1] Research Methods in Ecology, 25, 145.

along three parallel lines, which have been designated
as (1) natural experiments, where advantage is taken
of natural movement into new habitats, (2) habitat cul-
tures, where reciprocal plantings are made in original
and new habitats, and (3) control cultures, where the
experiments are carried on in plant-houses, where they
can be controlled and directed at will.   In addition to
this, definite experiments for the determination and pro-
duction of constancy are of fundamental value.   In
regard to the evaluation of the new form when once
produced, it will suffice here to state that this should be
concerned both with the individual and with the group
of individuals.   The proper determination of the latter
is the task of biometry, when it has attained the neces-
sary development.

For the preservation of the results obtained by the
ecologic methods briefly sketched above, an *evolution
herbarium* is proposed.   It is felt that the usual taxo-
nomic herbarium will have its usefulness restricted more
and more to the preservation of types, and to the pur-
poses of instruction.   The evolution herbarium will be
the record of field observations and experimental results.
A species or a form will be represented in it by all the
variations that can be discovered, and each variation by
a large number of individuals.   The new forms produced
by nature, and by experiment in nature or under control,
will likewise be adequately represented.   This repre-
sentation will take the form not only of the usual dried
specimen, but of photographs, drawings, slides, pre-
served material, etc.   With all this, however, the evolu-
tion herbarium is still to be regarded as a record merely.
It is not to replace the taxonomic herbarium as a mass
of working material to be shuffled about and made into
species.   It is a repository of species and forms when
they have finally been determined by experiment.

IV. Nomenclature and Treatment of New Forms

Enough has been said to indicate clearly the ecologist's view of species, both valid and otherwise. He is vitally interested in the species' ancestry, its method of origin and the factor concerned, as well as in the result, which is the species or form itself. Until his experimental study of these points makes it possible to distinguish species from minor groups, or shows that the species concept is a mistaken one, it is useless to debate whether the resulting form is a species or not. In fact, the status of the result must await the determination of ancestry and origin in every case, and we may well call all the results forms until this has been done for each.

The question of ancestry resolves itself at the outset into one of old forms or of forms newly produced. The production of a new form from an old or existing one by properly checked experiment at once gives the ancestry of the former. Here, where the whole experiment is under our control from beginning to end, we may concentrate our attention upon the method of origin and the factor concerned. The discovery of the ancestor of an existing form or species is often a much more difficult matter. Until the ancestry is determined, it is useless to try to ascertain the method of origin, and the factor. When the form bears the distinct stamp of sun or shade, of a wet or dry habitat, or of hybridation, etc., our search is narrowed at once to deciding what species gives the most promise of being the parent form. When there is no distinct stamp, we must first look for the most promising species, and then try the various methods and factors experimentally until the form sought is produced. How often the ancestry and origin of accepted species can be worked out in this way remains to be seen. Results already obtained show that this method works perfectly in the few cases tried, and that it may be expected to prove successful in many cases. When a complete series of trials of suspected parents does not give the form sought, it seems fair to assume that these and the species

sought are more or less coordinate.   In this process, it is probable also that light will be thrown on the question of their derivation from a common stock or from two or more stocks.

The four methods by which new forms originate have been discussed before this society in a paper read last year.   These have also been given in some detail in print[2] and are so generally well known to botanists that detailed consideration of them is unnecessary here.   These four methods are adaptation, mutation, variation and hybridation.   Variation alone has not yet been certainly established by experiment as a method by which new forms originate, but the evidence of it is so strong that it amounts to presumptive proof.   It seems certain that for plants at least it is not the principal method, as Darwin thought, and that it is probably much less important than adaptation, and probably also less important than mutation.   It is, however, a much more obscure process, and it is impossible to tell in the absence of any critical experiments just what it is, or what its importance may be.   Darwin has said: "I have spoken of variations sometimes as if they were due to chance.   This is a wholly incorrect expression.   It merely serves to acknowledge plainly our ignorance of the cause of each particular variation."   The exact measurement of habitats has made it clear that minute variation in the factors of the habitat is a very important if not the ruling cause in the production of minute variations in structure. In the case of the minute initial variations shown by the individuals of a group, it is impossible to tell at present how much is due to heredity and how much to causal variation of the habitat.   It seems probable that the former may control in some forms, and the latter in others.   Furthermore, while hybridation stands apart sharply from the others as a process in which existing characters are mixed in some degree, it is becoming more and more probable that adaptation, variation and muta-

[2] Research Methods in Ecology, 147; Plant Physiology and Ecology, 185.

tion are only different phases, perhaps merely differences in degree, of the fundamental struggle between heredity and environment.

Forms arising by adaptation have been called *ecads,* those from variation, *variants,* and those from mutation, *mutants.* With the familiar term *hybrid* for the product of hybridation, we are able to designate in a general way the forms originating by the four methods. The ecologist, and sooner or later the whole botanical world, must have some definite way of naming each particular form. It is possible to take no further thought about the matter, and allow this nomenclature to grow in the same random, unscientific fashion that nomenclature has always grown. It seems highly desirable, however, to consider the requirements of the case, and make suggestions as to the best method of meeting them. The first essentials of a name are that it should be as short and as significant as possible. For our present purpose, the name of each form should indicate the ancestry and the method of origin, and, when it is known, the causal factor. Many ways of securing this result have been considered for each method of origin. This may be illustrated by the following list, showing several possible ways of naming the shade ecad of *Galium boreale.*

1. *Galium dubiosum* n. sp.
2. *Galium boreale dubiosum.*
3. *Galium boreale.*[2]
4. *Galium borealades.*
5. *Galium boreale scias.*

The first method, which is that of descriptive botany at present, indicates nothing of ancestry, origin or factor. The second gives merely the ancestry, as does the third. The fourth gives both ancestry and method of origin, the patronymic suffix *-ades* referring to ecad. The use of a suffix has much to commend it, particularly the fact that it makes it possible to designate the forms of a species by means of a binomial. Its use, however, has practically been made impossible by the senseless names

that have too often been given species. The fifth method, though requiring the use of the trinomial, is the best. It has all the brevity possible, and yet indicates ancestor, method of origin and factor concerned. It is interesting to note that this problem was worked out in 1902 in essentially the same fashion.[3] The shade form of *Galium boreale* was then called *Galium boreale hylocolum.* The present method has the advantage of brevity, and of referring directly to the causal factor concerned in producing the ecad rather than to the habitat as a whole. It is a relatively simple matter to recognize and produce sun and shade ecads, wet and dry ecads, but ecologic analysis can hardly go further at present. Consequently, the use of *scias, helias, xeras* and *hydras,* denoting respectively shade form, sun form, dry form and wet form, will not only enable us to designate all new ecads briefly and conveniently, but it will also reveal the ancestor, method of origin and causal factor at a glance.

After much puzzling, it seems that it will prove difficult, if not impossible to improve upon the conventional method of designating hybrids, viz., *Galium boreale* $\times$ *trifidum.* Until more is known of variants, it is proposed to designate them by a brief and applicable trinomial term, *e. g., Galium boreale exiguum.* While this is the usual trinomial, it would at once reveal the method of origin, as well as the ancestor, by virtue of the fact that the other three methods of origin have their proper trinomial form. In our present knowledge of mutants, it seems impossible to take the cause into account. The suggestion is accordingly made that the mutant be named with reference to its most striking characteristic, the trinomial term to bear the prefix *per,* very, referring to the saltatory nature of mutation, and thus denoting the method of origin. The value of these suggestions may be indicated by comparing the trinomials thus formed with the corresponding binomials.

[3] Herbaria Formationum Coloradensium.

Cerastium oreophilum == *Cerastium strictum scias:* ecad.
Verbena intermedia = *Verbena stricta* ✕ *hastata:* hybrid.
Aquilegia jamesii = *Aquilegia cœrulea peralba:* mutant.
Machæranthera aspera = *Machæranthera viscosa aspera:* variant.

In concluding, the ecologist will confess frankly that
he does not know what a species is. On the other hand,
he is certain that he knows some of the things it is not,
and that the species of the descriptive botanist comprise
several widely different things. Just what these are and
what their relation to species, if there are such, is a
matter to be decided by experiment alone. The ques-
tion of what a species is can not even be answered pro-
visionally until a sufficiently large number of experi-
ments have been made to indicate the regular procedure
in the origin of plant forms and to reveal the principles
that control it.

AN ECOLOGICAL ASPECT OF THE CONCEPTION OF SPECIES

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In the discussion of this question I do not feel myself hedged in by any limitations, since no one pretends to say what are the bounds of ecology. Indeed, to define a species may be regarded as an easy task, compared with the task of one who sets out to define ecology. And so this occasion affords me a pleasant opportunity to present some views for which I have long desired an audience like this.

It is coming to be realized that the problems of physiology and ecology are essentially identical, not alone in the matter of the species concept, but in all respects. Physiologists and ecologists have come to feel that the experimental method furnishes the only adequate test for determining the validity of species. The method of approach has differed with the point of view, and it is the physiologist who has given most emphasis to the fundamental importance of experimentation. The ecologist, on the other hand, has brought in the rich contributions of field observation. It is only recently that each has recognized the imperative necessity of the method of the other, and it now seems possible to predict that the fundamental method of the future is to be field experimentation combined with observation. No one realizes so well as does the ecologist the inadequacy of laboratory experimentation in the settlement of field problems. The ecologist feels that the species problem is essentially a field problem, and hence incapable of final settlement, either in the herbarium or in the laboratory. Yet it is the exact methods of the laboratory carried into the

field that give promise of the solution of the problem of species.

Perhaps no phenomena bring the principles just enunciated into more clear relief than do those of natural selection. Many species must be born that never have an opportunity to survive, owing to their lack of adaptation to the surroundings in which they originate. The mutants of *Œnothera lamarckiana,* though developed under essentially similar conditions, do not appear equally adapted to the environment in which they first appeared; had they been left to themselves, some mutants would have perished, while others (and perhaps especially *Œnothera gigas*) might have lived. The citrus hybrids, developed in government experiments in Florida, form another group of new forms, some of which are best adapted to one climate, and others to another. Since, therefore, no necessary adaptive relation must exist between a new species and the region of its birth, it is clear that the laws of selection determine the success or failure of new species. The interpretation of selection is a field problem, an ecological problem. A theoretical plant species may be produced in the laboratory, but the real species that make up the vegetation of the world are developed and must be studied out of doors.

One of the noblest aims of ecology is the destruction of many of the "species" of our manuals. Where the critical study of species is confined to the herbarium, it often happens that ecological varieties or habitat forms are given specific rank. An excellent instance of this is seen in the case of *Polygonum amphibium* and *P. hartwrightii.* The latter, which looks wonderfully different from the former in herbaria, can be developed at will by growing *P. amphibium* on land instead of in the water. Not infrequently a plant may be found on the edge of a pond, showing branches in the water that would commonly be referred to *P. amphibium,* and aerial branches that would be regarded as *P. hartwrightii.* Bonnier's classic experiments, whereby many alpine

plants were shown to be capable of being developed into well-known lowland species in a single generation, illustrate a phenomenon similar to that exhibited by Polygonum.   It is likely that our manuals contain many so-called species, such as these, which await reference to ecological varieties.

Having eliminated habitat forms from the rank of species, and having disposed of the influence of natural selection as a destroyer of many incipient species, it remains to discuss the varied ideas concerning the real or supposed species that remain.   In the main it may be said that there are two opposing conceptions of species that are to-day struggling for mastery in the realm of biologic thought.   The more prevalent idea, dating in its essence from the time of Darwin, has been that species are artificial creations, mere matters of convenience in the classification of the organic world, arbitrary concepts that have no great and enduring reality. Partisans of this view hold to the doctrine of continuity, maintaining that all species have been connected with other species by a series of intergrades, and that there is no vital distinction between variation and mutation.   If, indeed, many species, such as the sassafras, differ widely from all other known species, this is because of the elimination of intergrading forms.   In the case of Sassafras, this idea is strengthened by the evidence furnished by fossil forms.   In somewhat striking contrast to this concept of species stands the idea that species are entities, which arise by discontinuous variation or mutation, and which have their full specific value from the start.   Nor does time change specific form by any slow gradations; the species at its death shows no essential difference from the species at its birth.   In many instances, at least, these species are of lower rank than the Linnean species, and have been known as small or elementary species.   As a rule those who hold to the latter species conception are more prone to appeal to hidden "internal" causes in explaining the origin of new species, while environmental

factors in evolution are more commonly held as dominant
by those who regard species as indefinite things gradually
evolved from other species.   In this connection it is
curious to note that the idea of a species as an entity,
now held by most mutationists, has much in common
with pre-Darwinian notions of special creation; it seems
to be in part a return to former conceptions of a rigid
nature.   On the other hand a new idea of species content
is set up.   Both pre-Darwinians and Darwinians agreed
that *Draba verna* is a species, but the new school would
maintain that under this name are masquerading a hun-
dred odd real species.

There are, then, two radically different conceptions of
species now current, one of a rank as much higher than
the other as the genus is above the Linnean species, or
the family above the genus.   Ecological observations
support both views, but it is especially the experimental
method that has made things clear.   Whether or not
one calls them species, it is evident that the genus
Œnothera contains a number of entities, sharply defined
from one another.   In such genera as Salix and Aster
there is reason to believe that species do not thus differ
sharply, but that they are connected with one another by
all but imperceptible gradations; at any rate this condi-
tion exists in Leptinotarsa, as conclusively shown by
Tower.   It seems impossible to homologize species in
Œnothera and Leptinotarsa.   It appears that the method
of evolution in various groups of plants and animals is
radically different, and it follows as a corollary that
what are called species in these various groups are neces-
sarily not homologous.

In the light of these views the task of the taxonomist
is seen to be most difficult; for the convenience of biol-
ogists, he must reduce to common terms things that are
unrelated; he must homologize things that are not homol-
ogous.   In such a dilemma there seem two courses open:
(1) The Linnean species concept, that has ruled both
before and after evolution was accepted by biologists,

may be abandoned. The elementary species then becomes the species of taxonomy. Something akin to this has already taken place in certain genera, notably Cratægus, Viola and Sisyrinchium. Those who take this attitude should abandon the year 1753 as a starting point for specific nomenclature, since a new conception of species demands a new datum line. Possibly this datum line is furnished by the experimental work of Jordan on *Draba verna*. Such a revolution would of course be appalling in its consequences. The present status of Cratægus, perhaps, gives an index of what is to come, if this idea is accepted; where now we have dozens of species, we may expect hundreds or even thousands. We may even expect the appearance of a taxonomic daily newspaper with its hourly record of new species and their fluctuations, comparable with market quotations in a period of financial panic. (2) The alternative is to retain the Linnean species concept as a working theory, employing trinomials for elementary species. Thus we should speak of *Œnothera lamarckiana rubrinervis, O. lamarckiana gigas,* etc. One great advantage of following this method would be that we should secure all the advantages of the newer critical study of such genera as Cratægus and Sisyrinchium, and at the same time tie the new work to the old in such a way that those not taxonomists could appreciate the general significance of the results. Very few except Cratægus specialists could tell offhand anything about *Cratægus ellwangeriana* or *C. champlainensis,* but if these forms were denominated respectively, *C. mollis ellwangeriana,* and *C. mollis champlainensis,* many would know their general affinities, In the case of intergrading species without well-defined specific boundaries, the only course is to retain the trinomial for varieties, much as has been done in the past. If it is wished to distinguish between varieties and elementary species, the expression var. might precede the varietal name, as is the custom now with many.

It is to be hoped that the taxonomists, and particularly

those taxonomists who have sinned in the much making
of species and those who have made a so-called critical
study of plants without any adequate training in the
general principles of botany, will reform their ways.
In truth, they must reform. No longer may each man
be a law unto himself. Nor is it right that any group
or coterie should make rules and regulations that run
counter to the expressed opinions of a world botanical
congress. It is doubtful if any single botanist agrees
with all of the taxonomic expressions of the Vienna Con-
gress; it is even possible that some agree with none of
its provisions. However, it registers a general consensus
of opinion, agreed upon by those who thought the con-
gress far too radical, and by those who thought it far
too conservative. It marks a step in the taxonomic
progress of the botanical world, and there is no surer
way to lead toward further progress than in abiding by
its provisions; on the other hand, there is no surer way
of ensuring the continuation of the taxonomic chaos, of
which we have had far too much, than in setting up indi-
vidual or even provincial or national codes in opposition
to a world code. An American school of taxonomy is
an anomaly, since many species are world-wide, and
should have world-wide names; even the local species
should be delimited in accordance with international
rules.

Taxonomy must be scientific. It must require for its
devotees a training as rigid as that required by profes-
sional workers in morphology, physiology or ecology.
Species-making by taxonomic tyros must be abandoned.
The requirement of Latin diagnoses, though regretted
by many of us, may be of help in checking the voluminous
contributions of amateurs. In the future it must be
recognized that the final test of the validity of species
is experimental, and taxonomists must work no less in
the herbarium, but more in the field and in the garden.
If the taxonomists of the future fail in these respects,
a hard but certain fate awaits them. The world of

morphologists, physiologists and ecologists has borne with them patiently and long, and has deferentially abided by the specific determinations of the taxonomists. The recent ebullitions of the taxonomic radicals have evoked in botanists in general successively dissatisfaction, contempt and rage.   These things will not be endured much longer; a little more and the sinning taxonomists will be "cast out into the outer darkness where there shall be wailing and gnashing of teeth."

DISCUSSION OF THE SPECIES QUESTION.

At the close of Mr. Cowles's paper the chairman invited those present to discuss the question. The following remarks were made:

Mr. J. M. Coulter: I find myself in some particulars agreeing with every speaker, and it seems to me that there are enough elements in common in all that has been said to enable us to reach some sort of working basis. One thing agreed upon in all that has been said is that nature makes individuals and men make species. This means that in a certain large sense the individual is the unit to be recognized. At the same time it is evident that the attempt to record such units on the basis of any present scheme is entirely out of the question. While it is clear that we are approaching greater uniformity in our conception of species, we shall not reach agreement until we know more definitely the influence of ecological and physiological factors, if we may separate them for the moment, upon structures. But until this knowledge becomes more exact, how shall records be made? We must have some temporary and effective method. We all appear to recognize the fact that the indefinite multiplication of names of species must be stopped sooner or later, and the sooner the better; for we are getting the record into a condition that makes it unworkable. It seems to be the belief of every speaker that something must be done, and that the conception of a species must be modified eventually. It is quite evident that we are in no position as yet to formulate definitely what we shall agree to call a species, and in the meantime it seems to me the suggestion made by Dr. Britton is a very workable one. It gives to every one the opportunity to distinguish and record forms clear down to individuals if he chooses; and at the same time

it removes the grievous burden of a great multiplication
of names.   It seems to me that the suggestions of Dr.
Bessey and Dr. Britton almost meet at this point.   In
effect, it means to continue to name easily recognized
forms, calling them species if desired; and then by a
system of numbers to indicate the more refined distinc-
tions.   This avoids the great multiplication of names
and secures an exact record.   This method has been
developed so effectively in the cataloguing of stars and
books that it could be adapted for plants without serious
trouble.   I would ask Dr. Britton how much this scheme
would reduce the number of published names.

Mr. N. L. Britton: I do not know.   Those that have
been published up to this time it would reduce probably
two thirds.

Mr. J. M. Coulter: A reduction of the names to one
third would be a good start, and I think we had better
hold Dr. Britton to his idea.   I think we can get together
on this suggestion, so that all botanists can recognize the
ordinary forms and remember their names, and the taxon-
omists can record the more refined distinctions.   I had
not heard of this proposition before, but at present it
appears to me to be desirable and workable.

Mr. J. B. Pollock: I should like to say a word along
the line of work upon which Dr. Arthur has presented
some thoughts to you, but I think we can go a little fur-
ther than Dr. Arthur did in his argument in regard to a
definite method of getting at species from the physiolog-
ical basis, and the people who are nearly ready to begin
that, I feel sure, are those who have worked with the
fungi from the cultural side.   In talking with a number
of men, who are interested in that side of the work, in
the course of these meetings, I have been impressed with
a fact the importance of which has been growing upon
me in my work alone, that the men who are doing that
kind of work are feeling the absolute necessity of doing
something definite exactly along the line which has been
indicated by almost all the speakers here in a general

way.   Now, what I mean is the kind of work which was
reported in the botanical session this morning on
Penicillium and its relation to definite culture media,
and I believe in the very near future we shall be describ-
ing species, of many of these fungi in a definite relation
to culture media.   A species will be a group of those
organisms which show a certain combination of morpho-
logical characters when grown upon a medium of definite
and known composition.   The type of the species in-
volves a type medium, and the fluctuating variations
must be determined by the use of a series of such media.
Considerable work in this direction has been done, but
the method has not yet been well adapted to taxonomic
description.   I think we are ready now to do this work
from a strictly taxonomic point of view.   That will be
doing exactly what at least four of the speakers have
advocated, but they did not tell us in detail how to do it.
These fungi are particularly suited to this kind of work
for several reasons.   In the first place, they are small
in size and we do not need a garden in which to grow
them; we can grow them in a test-tube.   In the second
place, they reproduce exceedingly rapidly and we do not
have to wait a year or ten years in order to get them to
produce new generations.   They may do that in a few
hours, or at most in a few days, so that we can produce
generation after generation, while the man who is work-
ing with flowering plants is waiting for one generation
to develop.   Hence these plants are favorable material
with which to begin the kind of work which seems to be
demanded, namely, the union of the morphological and
physiological factors in the description and delimitation
of species.

Mr. T. J. Burrill: I do not know that I have anything
very definite to say, but I am somewhat conscious of a
feeling that I am glad that I am not a taxonomist this
afternoon.   The taxonomist has certainly suffered this
half day.   It was said here a few moments ago that there
had been no progress along the line of the systematist;

that we have developed greatly elsewhere, but in this
particular we have remained medieval or worse than
that.   I think we have abundant evidence right here that
there has been progress.   This meeting this afternoon
would have been no more possible a dozen years ago
than it is now to separate out the species of Cratægus by
somebody who has not studied them during that time.
There has been something working.   People have been
finding that there is something besides names and dates;
something has occurred since 1753.   It looks to me as
though it were hopeful.   If there is anarchy, more of
that than anything else, it is a pretty good beginning to
start something that is not anarchy.

However, I feel sure I shall not give up everything in
regard to our common notion of species and species'
names.   I do hope that I shall know the white oak under
its proper name hereafter when I see it, and a few other
things like that; and I think it is really important that
when we speak about certain things, of certain effects
and relations, we do understand what we are talking
about and that others may also understand.   I think
it does make a difference as to whether we continue the
use—to take Dr. Arthur's first illustration—the definite
use of such terms as *Bacillus anthracis* and *Bacillus
typhosus,* and the rest of them.   If a writer is going to
discuss a subject in which these organisms play a part
and one that is vital to our existence and welfare, it is
surely desirable that we should have a correct interpre-
tation of what he means when he uses these terms.   I
believe we are pretty near that meaning in regard to the
common organisms in the group of bacteria, so that we
know pretty well what is meant when such names as
those above are mentioned, though nobody will deny that
included among the organisms to which the names ap-
ply there are considerable differences.   They are dif-
ferent in their sizes, if you come down to microbe meas-
urements; they differ certainly in their growth upon
different media, and I do not see why the physiological

effects may not just as well enter into the species idea
as the morphological characteristics, if we can get them;
but I do not know how we are going to get them for such
plants as forest trees.   In the case of the white oak, we
have got to take the morphological characteristics alone,
so far as I see.   We can not plant the seeds and witness
the trees as they develop in their various stages until
they produce seed again.   But in case of the lower forms
with a generation a day, we can certainly do that, and
I think we ought to do it for specific characteristics.

Let me say, what I am most interested in is that we
shall know some things yet by some very well known
names.

Mr. E. G. Hill: As we have had considerable talk
from the pulpit, perhaps a little experience from the pew
in regard to species might be of use.   In 1874, I came to
that part of Illinois which is now embraced in the city of
Chicago, and the year after I began the study of the flora
of the region, the sand region (it was all sand then),
particularly this dune region east of the city, and there
has not been a year since that I have not been out there
more or less.   Now, I have not been over every foot of
it, but with regard to this plant, the *Polygonum amphib-
ium* that has been cited, I always until about 1890 or
1895, I can not give the exact year, I always saw *Poly-
gonum amphibium,* I never saw the other kind.   At that
time I noticed this hairy plant, with shorter internodes,
growing on dryer places.   The exigencies of the expand-
ing city and manufactures outside of it led to the partial
drainage or entire drainage of considerable areas of our
dune flora.   The underground parts of *Polygonum am-
phibium* are pretty extensive.   I never satisfy myself
without digging up the entire under part of plants, or
digging up the root—I can follow a root ten feet, if
necessary.   When those wet places were drained, the
roots persisted in the sand, and the plants while pre-
serving their full form when in the water, would be hairy,
and you can trace them all the way from the water up,

may-be twenty to thirty feet from the edge of the water,
making their way even along paths or roads.   Now, I
want to say, I do not know that they did not exist before
that, but I never noticed them until then; and not a mile
or two miles from here, if there are vacant lots, you will
probably find *Polygonum hartwrightii* in a drained
slough, where twenty to twenty-five years ago you would
not find anything of that kind, but you would find
Polygonum amphibium.   It seems to me that is the way
in which it might have originated here.   This experience
extends from about 1875, and although I gather from it
that it was not here before, I believe that it made its
appearance not far from 1890 to 1895.

Mr. G. H. Shull: In one sense the recent discoveries
in the realm of variation and heredity appear to lead
to a backward step in the concept of a species, since the
view of the naturalness of species to which these discov-
eries lead, resembles the earlier view.   Upon a com-
parison of the basis of this conception, however, in the
time of Linnæus, with the present situation, the contrast
becomes sufficiently striking.

At that time no cognizance was taken of the importance
of variations.   When variations were first fully taken
into account, about the middle of the last century, they
were apparently conceived to have no natural limits, and
in consequence, no form-group could have natural limits.

The demonstration that variations have natural limits
has shown that the lowest grade of form-group is a
natural group of individuals differing from each other
only by fluctuations.   It appears to me that the able dis-
cussions to which we have listened might all be reduced
to the question of the desirability or feasibility of looking
upon these *ultimate, natural form-groups as species.*
This question largely rests upon the question of utility,
and herein lies our difficulty in reaching a universally
satisfactory conception.   To the maker and keeper of
herbaria and to the field naturalist, utility requires that
species shall be separable by characters which may be

recognized by a more or less careful examination of a
single individual of unknown ancestry. To the experi-
mentalist, whether he be a physiologist, an experimental
morphologist or a pedigree culturist, such a conception
of species makes them of no utility, and this is also
largely true with students of cytology, anatomy, etc., who
study the morphology of structures not externally visible.
As a student of variation and heredity from the experi-
mental side, I hold that the *natural* group is the only one
that can be of any utility to any one but the herborizer,
but I do not insist on the privilege of calling this natural
group a species. That matter is entirely immaterial.
To avoid confusion, we are now calling these groups
elementary forms, but this expression is unnecessarily
cumbersome for the constant use the conception must have
in the future literature of botany, and I hope that some
one will come forward with an acceptable short designa-
tion for these, in case the herborizer succeeds in checking
the trend of development of the conception of species
from an arbitrary to a natural one.

Experimental evidence at the present time shows at
least two grades of form-groups. These were recognized
by Dr. De Vries under the names, elementary species
and varieties. By "varieties" De Vries indicates those
forms which differ from their nearest related form in
one or more characteristics, which behave according to
Mendel's law upon crossing with it. As taxonomists
have definitely abandoned the use of the term "variety"
to the horticulturist, we need a new word with which to
speak of this very definite class of forms. As we have
taken liberties with the name of Mendel in the formation
not only of the adjective "Mendelian," but also the verb
"Mendelize," there seems to be no reason why we might
not go farther and call these Mendelian varieties Mendel-
ities. These Mendelities are hangers-on of species, and
corresponding Mendelities may belong to many different
species, as may be illustrated by the frequency of occur-
rence of white-flowered or albino forms, which differ

from their corresponding pigmented forms in no other
character but that of pigmentation. Whether Mendelities
may in any case be the initial modification leading to new
elementary species is not known, but I believe that we
are not yet warranted in so considering it. But elemen-
tary species and Mendelities are certainly natural entities
and must be used as the physiological units of form.

MR. J. A. HARRIS: It seems to me that while the sys-
tematists are receiving the congratulations of morphol-
ogists and ecologists, it will be well for us to remember
that he "that is without sin" among us "should cast
the first stone." I think in the present state of biology,
the morphologist and physiologist and ecologist have
some points to learn from the systematist, and that the
morphologist, physiologist and ecologist are to some ex-
tent responsible for our present inadequate knowledge of
species.

The taxonomist has worked out a very careful scheme
of recording his observations; he feels himself bound, in
preparing a monograph, to cite all descriptions. It is
perfectly easy to take a well-prepared monograph and to
follow out the earlier literature of any form. If, on the
other hand, one turns to morphological and physiological
writing, he will find it is a difficult task to locate the work
which others have done on the same species. It seems
to me that if the taxonomist is expected to make use of
experimental and ecological data in his limitation of
species, he should be given the data, by those who are
doing such work, in a form in which he can use them.
Take, for instance, our ecological papers. An ecologist
works on a certain region and refers to a number of
species definitely, and to a larger number of species in-
definitely, grouping them as grasses, sedges, asters, etc.
How is the taxonomist to utilize such data. The work
of the ecologist should be specific and comparative. He
should be explicit in his statements concerning the form
and life conditions of a species in his own region, and
he should refer to the literature in such a detailed fashion

as will enable the systematist to determine the characteristics and the environment of the same species in another region. I think the morphologist, too, must adopt the practise which the systematist has found indispensable. He should cite in a clear but condensed form all the pertinent morphological literature for each of the species which he treats. The recognition of this obligation would, I believe, do much to raise the standard of our published work, and it would place at the disposal of the systematist a mass of data which he ought to use to great advantage.

Mr. A. E. Hitchcock: I wish to call the attention of the ecologists to one very important method by which they may greatly aid the taxonomists. The former are doing much careful work in studying the ecological relationships of plants, but in order that this work may be checked up and be available to taxonomists it is necessary that specimens of the species studied should be prepared and deposited in a public herbarium. Unless such a permanent record can be made the statements concerning habitat, variation and other ecological data are of little value to the systematist, because they can not be verified. Such verification is especially necessary because the ecologist is not likely to be sufficiently familiar with all groups of plants to pass authoritatively upon their botanical names. Even when the plants are submitted to taxonomists for identification it may happen that errors occur. Data based upon specimens available in public herbaria would aid ecologists themselves to coordinate their work. Taxonomists will be glad to avail themselves of all serious work done by ecologists when the data can be definitely connected with preserved specimens.

One other point. I wish to emphasize the necessity of field work in determining the limits of species. If possible, taxonomists who are monographing groups of plants should study these plants in the field. The botanist can determine usually to his own satisfaction the limits of variation of a single species in a given

locality.   The herbarium then becomes a record of his
field observations.   Much good work can be done in the
herbarium, but when coordinated by abundant observa-
tions upon the plants, as they occur in nature, the conclu-
sions are much more likely to be correct.

Mr. G. H. Shull: I would like to say one word in re-
ply to Mr. Hitchcock's remarks regarding what we know
about variations when we seen them in the field.   It is
my experience in the cultivation of things brought in
from the field during the last four years, that we know
nothing about the significance of variations in the field
as to their bearing upon the question of the species, if
by species we mean a continuously variable group, be-
cause in some instances we find that very distinct varia-
tions as seen in the field are immediately lost when the
individuals possessing them are grown under uniform
conditions.   We find, on the other hand, that equally dis-
tinct, or even less distinct variations—as determined en-
tirely by an estimate of the difference in form—are re-
tained with absolute permanence so far as one can
determine by three or four years of culture under like
conditions.   Now, how we can tell without an experi-
mental basis for the estimation of the meaning of varia-
tion in any particular species, what is the significance
of those variations as we see them in the field, I am at a
loss to understand.

SHORTER ARTICLES AND CORRESPONDENCE

OTTER SHEEP

THE following account of the "otter" sheep occurs in Vol. III, p. 134, of President Timothy Dwight's Travels in New England and New York; New Haven, 1822. It is more explicit than any I have seen before, and may be of interest to naturalists. The date of the journey in which this account appears was about 1798.

Mendon, the township mentioned, is in Massachusetts, about eighteen miles southeast of Worcester.

"In this township, if I have been correctly informed, an ewe, belonging to one of the farmers, had twins, which he observed to differ in their structure from any other sheep in this part of the country; particularly the fore legs were much shorter, and were bent inward, so as distantly to resemble what are called club feet. Their bodies were, at the same time, thicker, and more clumsy. During their growth they were observed to be more gentle, less active, less inclined to wander than other sheep, and unable to climb the stone walls with which this region abounds. They were of different sexes. The proprietor, therefore, determined on an attempt to produce a breed of the same kind. The attempt was successful. The progeny had all the characteristics of the parents, and although they have since multiplied to many thousands have exhibited no material variation. I am further informed that the breed has been crossed with a breed of sheep common in this country; and in all instances to the date of my last information, the lambs have entirely resembled either the sire or the dam; and have never exhibited the least discernible mixture.

"These sheep are called the Otter breed from a resemblance to the animal of that name. Their flesh is said to be good mutton; and their wool not inferior to that of common sheep, either in quantity, length, or fineness. But their peculiar value consists in the quietness with which they continue in any enclosure. In a country where stone walls are so general as in many parts of New England, it would seem that sheep of this description must be almost invaluable."

C. L. BRISTOL.

NEW YORK UNIVERSITY,
March 18, 1908.

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NOTES AND LITERATURE

EXPERIMENTAL ZOOLOGY

Przibram's Experimental Zoology, of which Part I has just appeared,[1] is an enlargement of his brochure of 1904. It is the author's purpose to publish four other parts dealing respectively with Regeneration, Phylogeny, Vitality and Function.

The present volume brings together the modern experimental work dealing with the egg and embryo. The results are grouped under the headings of Fertilization, Egg-structure, Karyokinesis, Gastrulation, Developmental Mechanics and Influence of Environment. There is a very full bibliography, and sixteen partly colored plates. These plates contain many figures familiar to the student of modern literature of the subject. The figures are often too small and their arrangement in plates at the end of the book is not as advantageous as figures at suitable places in the text would be, nor would their simple character preclude their insertion as text figures.

The book will prove most useful, giving as it does a very complete résumé of the subject. The matter is treated in large part as a series of reviews under topic-headings of the results obtained by each author, and in the present state of the subject no other method is perhaps feasible; but while this treatment is satisfactory as a résumé of what has been done, it is not an arrangement that furnishes entertaining reading to the uninitiated.

At the end of each chapter the author attempts to draw general conclusions from the evidence reviewed, and inasmuch as these conclusions serve to register the author's point of view we may examine them in some detail.

The work of recent years on artificial parthenogenesis leads to the conclusion, in the author's opinion, that the cause that calls forth the further development of the quiescent egg-cell is to be found in the hastening of the vital processes already existing in the egg by means of the withdrawal of water from the

[1] Experimental Zoologie. Part I, Embryogenese. By Hans Przibram. Franz Deuticke, Leipzig, 1907.

egg. Normal fertilization is supposed to act in the same way. The evidence at hand does not appear to the reviewer to substantiate this generalization, because the shrinkage sometimes observed in the normal egg may be an effect of changes taking place rather than their cause, and because, in the second place, some of the most recent results, especially those with weak acids (Lefevre), can scarcely be interpreted on Przibram's view. There are some indications, on the contrary, that fertilization is a vital act in the sense that the sperm is a stimulus starting development in the same way that many external agents call forth the nerve impulse in a nerve. Here also in the nerve the same impulse may be called forth either by internal factors or by external agents. The intimate nature of irritability of living material remains, however, as much of a puzzle to the physiologist as to the embryologist.

The occurrence of visible inclusions in the egg,—pigment, yolk, granules, etc.,—leads the author to conclude that even before fertilization the egg is made up of different substances, which "guarantee" the subsequent development. We touch here on one of the burning questions of modern embryological speculation, for while certain evidence seems to show that different substances contained in the egg furnish a "guarantee" of diversity, still the central problem remains untouched, for few, if any, experimentalists will admit unreservedly that these materials are preformed primordia, or organ-forming substances in a strict sense, rather than that their presence is a condition that prejudices in certain directions the subsequent development. In other words we are still unable to state how far and in what sense the development is due to preformed materials and how far it is an epigenetic phenomenon depending on the relation of the parts to each other in a dynamic sense. It may be well in the present unsettled state of the subject not to prejudice these questions, for, there may be truth on both sides, since predetermination and epigenesis are not mutually exclusive possibilities, but rather complementary.

In regard to the location of the first cleavage plane, Przibram points out that this is "given" by the location of the segmentation spindle. The position of the spindle itself is the result of the egg structure, the geometrical form of the egg and the meridian of fertilization. The position of the spindle in any particular case may be due to any one or to more than one of these factors. The causal problems still remain to be considered.

The division of the centrosomes, the formation of the astro-sphaeres, the division of the chromosomes and of the cytoplasm, are not to be considered, according to Przibram's summing up, as constituting a series of causally connected events, but are the result of the same primary cause. While this point of view is sympathetic to the reviewer also, it should be clearly understood that we entirely lack sufficient evidence to establish such an attractive interpretation. Even if all these changes are the result of one cause, we can form no conception of what that cause may be. Our author's conclusion, at the end of the next chapter, to the effect that this common cause is to be found in a system of surface tensions, can scarcely be said to be at present more than the working hypothesis of a few thinkers of the school of developmental mechanics. One does not have to look very far for facts that are difficult to explain on such a view.

It is pointed out at the end of chapter VI. that the arrangement of the blastomeres conforms to Plateau's law of minimal surfaces. While it is true that such a law may appear to account for cell arrangement, we should not overlook the fact that a similar arrangement follows if the cells are simply flattened against each other by pressure from outside. Possibly also the mutual flattening—an active process—of the cells themselves might give the same arrangement. Therefore we do not know that surface tension plays even the chief rôle in the result. In fact, the author himself concludes in the next chapter that gastrulation is the outcome of chemotactic action, *i. e.*, of an active wandering of the cells. Such a conclusion appears to admit that the characteristic feature of formative processes may be responsive in its nature rather than chemical or physical.

The chapter dealing with the developmental mechanics of differentiation takes up the extensive literature describing the results of isolation of the blastomeres and of injuries to the egg. A very complete and impartial review is given here. Przibram attempts to interpret the results in the following way. Different chemical stuffs are supposed to be present in different zones of the egg and these lead to the differentiation of the different organs. If parts of the egg are removed and no rearrangement of the formative stuffs occurs, partial development takes place; but if a rearrangement follows, so that the parts recover their normal relations of position, a whole embryo of smaller size results. That the different parts of the egg play the rôle here

assigned to them can not be denied, and this is the simplest interpretation that embryologists have given to their results; but it is improbable that the differences between whole and partial development rest on this condition alone. The phenomena are really more complicated, as shown when whole development occurs even after the materials of the egg have become shut up within cells, and as shown in regeneration when a whole animal of smaller size develops from a part of the body of a fully formed organism.

The final chapter deals with the influence of external factors, and, although compressed into very small compass, most of the modern work is referred to at least briefly. The author's conclusion that external factors play in most cases only a minor rôle in development will be conceded by most students of experimental embryology. Nevertheless, important results have been already obtained from a study of external factors and our causal knowledge of the physiology of development rests in the main on evidence from such studies. Whether the formative changes are simply a complex of physiological relations or depend on factors not usually considered by physiologists is at present a question of opinion rather than of demonstration.

While we have found ourselves obliged in many cases to urge that many of the conclusions reached by the author still remain uncertain, and in other cases to take issue with the author's summaries of the present state of affairs, yet it should be repeated that the chief value of the book lies less in such generalizations than in the conscientious, full and exact review of the literature. The results so far obtained are marshaled forth in excellent order and the book is a valuable storehouse of materials, and will be found useful not only to those who do not have access to the original literature or time to digest it, but also to those who have felt themselves somewhat overwhelmed by the rapid development of this branch of embryology. The general reader, too, will find in this volume a well-balanced summing up of the more important results of the school of experimental embryology.

<div align="right">M.</div>

ICHTHYOLOGY

Jordan on Fishes.[1]—In a single large volume President Jordan presents "virtually all the non-technical material contained in

[1] Fishes. By David Starr Jordan, President of Leland Stanford Junior University. New York, Henry Holt and Company, 1907. Large 8vo, XVI + 789 pp., 18 colored plates and 673 figures. $6.00.

the author's *Guide to the Study of Fishes*. . . . His chief aim
has been to make it interesting to nature-lovers and anglers, and
instructive to all who open its pages.''

President Jordan can appeal to readers of any age. A de-
lightful account of the ''breeding habits of our smallest sea-
horse, prepared by the writer for a book of children's stories'' is
found on page 453. In the first chapter the author says that to
''understand a fish we must first go and catch one.'' It is
apparently with a boy companion that he starts for the old
swimming hole where they catch a sunfish—''a little, flapping,
unhappy, living plate of brown and blue and orange, with fins
wide-spread and eyes red with rage.'' In describing its life-
history, eating is said to be about the only thing a fish cares for.
The black swallower engulfs a fish many times larger than itself
(Gill) ; a single goosefish has been found with seven wild ducks
in its stomach (Goode) ; the pike is a mere machine for the assimi-
lation of other organisms; and the bluefish is an animated chop-
ping machine—an unmitigated butcher (Baird). Nevertheless
it is fortunate that the fishes can express no opinion as to two-
mile seines and some features of the canning industry!

A general description of the structure of fishes, of their
habits, adaptations, colors, distribution and economic value, of
the mermaid industry and the sea-serpent myths, form the first
section of the book—ten chapters.

In the remainder of the book fishes are considered systematic-
ally, from Branchiostoma to Malthopsis. In behalf of stability,
''the sole function of the law of priority,'' several familiar and
established names have disappeared. Lepisosteus replaces the
''more correct but also more recent spelling, Lepidosteus.'' The
general reader, interested in the fishes rather than their names,
will find that ichthyological terminology has been made as
unobtrusive as possible. Such terms as slippery-dick and pop-
eye grenadier make amends for considerable Greek, and common
names are freely used.

The reading of this book is not like a visit to a museum, or
even to an aquarium; there is more of out-doors about it. In
part this is due to quotations from anglers, classic and modern,
including Van Dyke's apostrophe to the ouananiche. Chiefly it
is due to the author's own experiences and such unexpected com-
ments as—''This is the noted Aweoweo of the Hawaiians which
used to come into the bays in myriads at the period of death of

royalty. It is still abundant, even after Hawaiian royalty has passed away.'' Or—''The coral reefs of the tropics are the centers of fish-life, the cities in fish economy. The fresh waters, the arctic waters, the deep sea and the open sea represent forms of ichthyic back-woods, where change goes on more slowly.'' Rarely there is a defective or ambiguous sentence, such as— ''Turner gives an account of a frozen individual swallowed by a dog which escaped in safety after being thawed out by the heat of the dog's stomach,'' but the book, as would be expected, is exceptionally well written. It is also well illustrated, and the figures (except Fig. 268) are carefully placed to accompany the text. They include a considerable number of photographs of living fishes, and eighteen colored plates, chiefly of fishes from the coral reefs of Samoa. The volume is attractively printed, except that Chapter XI, The Collection of Fishes, begins with a page on The Classification of Fishes (p. 157); whether the mistake is in omitting the rest of the chapter on classification or in printing its first page is not apparent.

An illustrated description of the changes in the external form of fish eggs during their development, further accounts of nest-building, and the quotation of Brooks' vivid descriptions of the salmon or shad, might perhaps have added to the popular interest in the book. It is, however, sufficiently large, and is full of authoritative information. It accomplishes all that President Jordan planned, and is a comprehensive introduction to a scientific knowledge of fish.

FREDERIC T. LEWIS.

(*No. 495 was issued on April 20, 1908.*)